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The Reproductive Behavior of the Green Sunfish, *Lepomis cyanellus*[1]

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(Text-figures 1-7)

INTRODUCTION

THAT the gonads of many centrarchids mature at intervals during the breeding season and that a population of centrarchids may have more than one breeding period during a season is known (Breder, 1936, 1940; James, 1946; and Kramer & Smith, 1962). No complete record, however, has been kept of the nesting habits of a population of sunfish throughout a breeding season. In addition, there is no published account of the reproductive behavior of the green sunfish although there are many descriptions of the breeding habits of other centrarchids (Breder, 1936).

The present study contributes information on the reproductive behavior of the green sunfish, *Lepomis cyanellus* (Rafinesque). Particular emphasis is placed on the frequency of nest construction by male green sunfish.

PROCEDURES

During two spawning seasons observations were made of green sunfish in four of the Gardner Ponds of the University of Wisconsin Arboretum. Ponds D and E were the largest. They were roughly rectangular in shape, had an area of approximately 2,023 sq. meters, a maximum depth of approximately 2 meters and were separated by a cinder dam. The cinders comprised the only firm substratum in the ponds. These ponds supported a large population of green sunfish, northern redfin shiners (*Notropis umbratilis cyanocephalus*), northern black bull heads (*Ictalurus melas melas*) and brook sticklebacks (*Eucalia inconstans*).

The two smaller ponds, designated as Theta and Delta, were also rectangular in shape, had an area of approximately 5 sq. meters and a maximum depth of 1 to 1.5 meters. Pond Delta supported a small population of green sunfish. There were no fish in Pond Theta until the Spring of 1961 at which time four male and six female green sunfish were stocked in it. Unlike the larger ponds, there was no firm substratum along the entire margin of these smaller ponds. An artificial spawning substrate was provided for the fish in Ponds Theta and Delta by placing a 1-meter-square box filled with cinders at the north and south ends of each.

The spawning grounds of Ponds D and E in 1960 and Ponds E, Delta and Theta in 1961 were visited each day during the breeding season. Each sunfish nest constructed on the spawning grounds was marked, described and the protocol recorded. Included in this account was the location of the nest, the time of construction, the duration of occupation and the time of desertion. A thermograph recorded the water temperature of the spawning grounds of Pond E during the entire spawning season. Daily maximum and minimum water temperatures of the two small ponds (Theta and Delta) were taken during the same period.

Male green sunfish in Pond Theta and Pond E were tagged at the beginning of the 1961 season and daily records were made of their nesting habits. In order to determine the factors in-

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volved in the recognition of the nest site by the male green sunfish, field experiments were performed.

Results

Sexual Dimorphism and Nest Construction.—During the breeding season a lateral series of dark vertical bars distinguished the female green sunfish from the male. This color phase was the same as that assumed by all green sunfish when extremely frightened. Males were more brilliantly colored and were larger than females. In addition, mature males possessed a prominent yellowish white line along the margin of the dorsal, caudal and anal fins. The white lines appeared on large males about a week before the first period of nest establishment; small males matured at a later date.

Male green sunfish constructed their nests in a manner characteristic of members of the family Centrarchidae. The male would rise vertically above the nest site and deliver a burst of vigorous outward thrusts with its tail. Each series of thrusts displaced some sand and gravel and gradually a shallow depression was formed. A male might spawn and dig in this fashion for one or two days, but after completion of the spawning period digging usually ceased.

Male green sunfish in the Gardner Ponds nearly always used the cinder and gravel areas to construct their nests and only rarely constructed nests along the muck margins. When a muck substrate was used, the male dug a deep nest, exposing the underlying marl. The nests most commonly occurred in unshaded areas which received a maximum duration of sunshine. The nests were constructed in shallow water seldom deeper than 35 cm.; small males constructed nests in water as shallow as 4 cm.

If available, areas sheltered by rocks, logs and clumps of grass were nearly always used for nest sites. Occasionally, abandoned sunfish nests were used by a male green sunfish as a site for a new nest, particularly if the nest was large and deep. I induced males to colonize new areas of the spawning grounds by scooping out depressions in the gravel which were deeper and larger than those they themselves constructed. These artificial nests were used throughout the spawning season.

A day or two in advance of nest establishment green sunfish congregated near the spawning grounds. In the beginning these aggregations were composed primarily of large males but as nests were established and spawning commenced, the area became congested with females and males of all sizes.

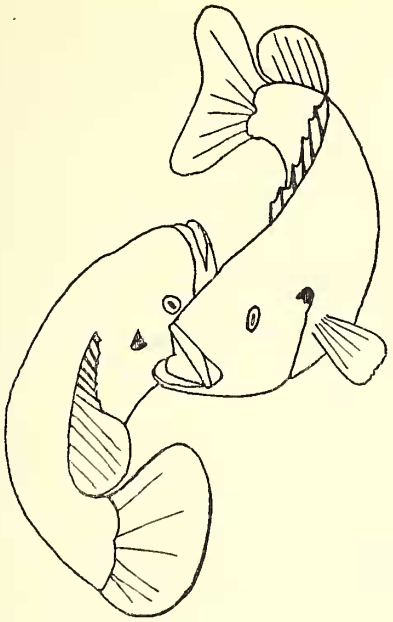
When males commenced spawning many females and non-nesting males assembled near the nest. The largest concentrations were formed around the periphery of the nests of the first males that spawned. In Pond E, which had a large population, I counted 114 sunfish assembled near the nest of a spawning male. Such spawning aggregations were visited, at one time or another, by most of the non-nesting males on the spawning grounds. Eventually some of the males in the congregation commenced digging nests in the vicinity of the original nest and a colony of nesting sunfish was established. As colonization began, the number of fish around individual nests decreased and became composed primarily of females.

Territorial Behavior.—Nearly all centrarchid males exhibit territorial behavior while they are occupying a nest. Witt & Marzolf (1954) reported that male long-ear sunfish, *Lepomis megalotis megalotis,* defended larger territories when their nests were isolated than when the nests were a part of a colony. I drew similar conclusions from my observations of nesting green sunfish. Within the colonies of Pond E, where nests were often less than 2 cm. apart, the males defended only the area encompassed by the nest. In Pond Theta, on the other hand, the distance between nests was as great as 30 meters and the males defended an area 1 to 1.5 meters in diameter. Sunfish collected around the nests of spawning males in Pond Theta but were not as close to the nests as they were in Pond E.

Fighting between males in the small ponds was never observed, but combat between male sunfish often took place on the crowded spawning grounds of the large ponds. The two male combatants pressed their open mouths to their opponent's operculum and, in this position, they rotated (Text-fig. 1). Only when the males were engaged in constructing nests and spawning did fighting occur, although they could be artificially induced to fight at other times. When I covered the nests of two males with stones in such a manner that their territories overlapped, a battle ensued.

Prior to spawning, nesting males sometimes permitted another male to swim through the nest or they ejected the male merely by nipping. As soon as the male commenced to spawn, he responded very aggressively to such intrusions and, with opercula spread wide, vigorously drove the trespassing fish from the nest.

During spawning periods male green sunfish were more active than during any other segment of their reproductive cycle. When a male was not engaged in spawning or chasing intruding fish he was usually swimming in circles inside the nest and taking frequent brief excursions



TEXT-FIG. 1. Fighting posture of two male *Lepomis cyanellus*.

outside. A male often punctuated his trips outside by nipping or threatening sunfish which were nearby. I observed one male during a ten-minute period execute five spawning acts, make ten trips in and out of the nest, threaten his neighbor once and gyrate in the nest 39 times.

Spawning Behavior.—If females were present on the spawning grounds, males usually commenced spawning on the day they constructed their nests or on the following day. If no females were present a male might continue to occupy his nest intermittently for as long as a week. The spawning period of a male sunfish occasionally extended over three or four successive days but usually was restricted to one or two. Spawning was accomplished in the manner typical of all centrarchids: the male and female circled in the nest side by side, paused momentarily and released sperm and eggs. The consummatory act took place when the female reclined on her side and vibrated while the male remained in an upright position. An isolated pair might circle and spawn in a nest for considerable periods of time but in crowded colonies the male frequently interrupted spawning to chase intruding fish. After spawning, the male expelled the female from the nest with a nip. Both sexes usually spawned with more than one individual. Occasionally a male spawned simultaneously with more than one female. While a pair of sunfish were circling in the nest another female entered the nest, aligned itself with the male, and when the first female rotated on her side the intruding female also slid beneath the male and vibrated.

Green sunfish did not spawn after dark but the aggregations of females and non-nesting males, along with the nesting males, remained on the spawning grounds overnight during spawning periods.

Once spawning commenced, rain and thunderstorms did not seem to curtail mating. I observed sunfish spawning on cloudy days and during thundershowers. This observation differs markedly from that made by Breder (1936) on the pumpkinseed, *Lepomis gibbosus*. He noticed that this species was so sensitive to changes in illumination it retreated to deep water during the passage of a cloud over the sun. I never saw green sunfish respond to clouds in this manner.

Sexual Recognition. — In connection with studies on the behavior of *Notropis umbratilis* (in preparation) a realistically painted latex sunfish model, cast from a mold of a male sunfish, was placed in various regions of the spawning grounds. The model was rotated in a circle (30 cm. diameter) at a speed of 6 rpm. by means of a small electric motor located in a submerged plastic case. Occasionally a few male or female sunfish assembled near the model. In one case, after threatening the model, a male commenced to circle with it in a manner which suggested spawning. The male interrupted his circling to chase away intruders and to execute a series of rapid digging movements near the model. This suggests that the circling of a female in a nest may be one of the stimuli by which a male recognizes a female. That sex recognition on the part of the male is based on the behavior of the female green sunfish seems likely as the male does not appear to distinguish between males and females when they are outside of the nest.

The approach of the female was nearly always hindered, rather than facilitated, by the male green sunfish. Any fish near the nest was threatened, sometimes nipped, but a female, unlike a male, continued to approach. As the female swam up to the side of the male they began to circle slowly and spawning commenced.

The presence of a male appeared to be sufficient stimulus to cause a female to enter a nest. Female green sunfish attempted to mate with nesting males in all phases of the male's reproductive cycle. During the latter part of the nesting period I occasionally saw females move from nest to nest in old sunfish colonies, often being expelled from every nest. Females some-

times darted beneath a male, immediately rotated on their sides and vibrated. Sometimes mating was accomplished in this fashion but often the male remained sexually passive, in which case the female was eventually driven from the nest.

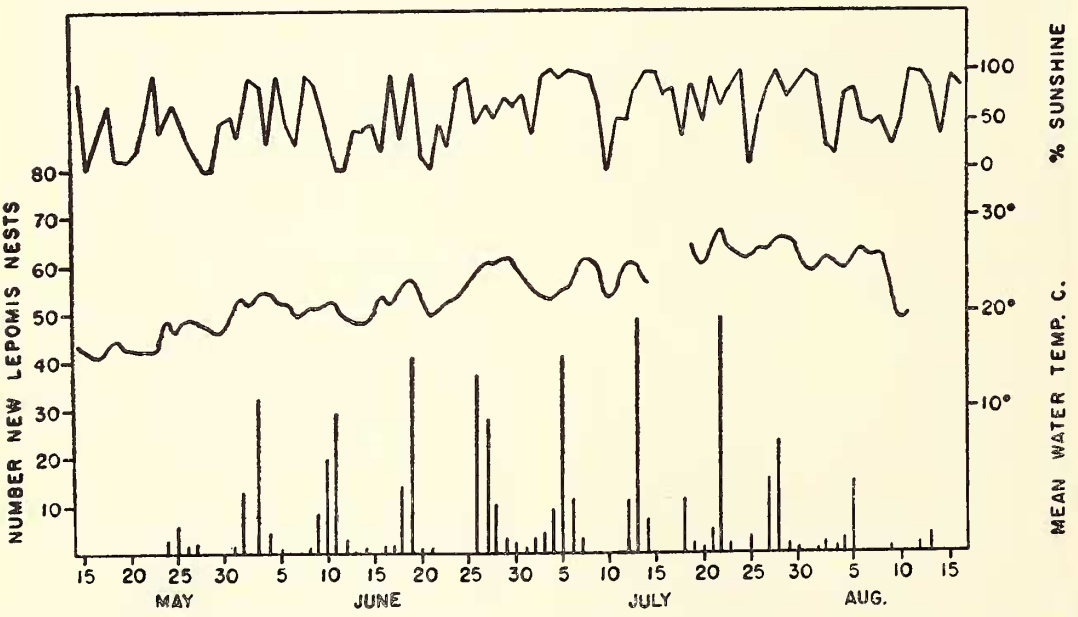
Females were most strongly attracted to and attempted to mate most often with males that had already started to spawn. As I have mentioned, spawning males, and perhaps unmated males excited by spawning males, behaved in a unique fashion. They gyrated rapidly and made frequent trips in and out of the nest. It may be that these additional activities made the spawning males more attractive to females. Breder (1936) believes that the gyrations of a male sunfish over a depression are the stimulus to which the females respond. I suspect that odors which may be released during the spawning act might also play a role in the attraction of females to the nests of spawning male green sunfish.

Breeding Cycles.—The breeding season of the green sunfish in the Gardner Ponds commenced in late May or early June, continued through June and July and terminated in early August.

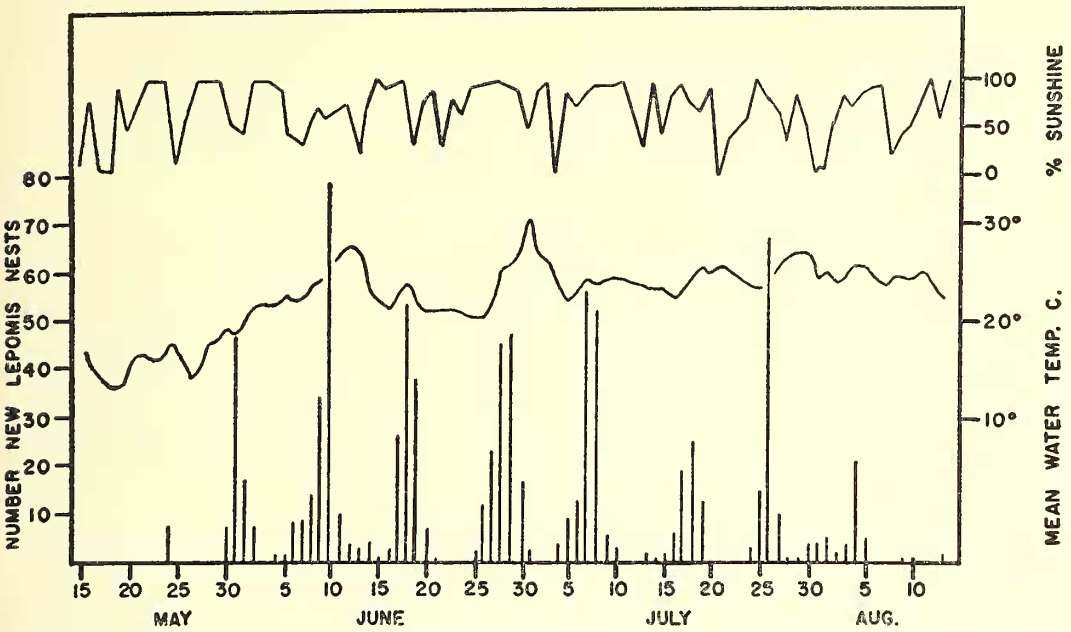
Daily tabulations of the number of nests constructed in Ponds E and Delta revealed that most nests were constructed during definite periods (Text-figs. 2, 3 and 4). The average frequency of the periods of nest establishment was every eight days in Pond E during the 1960 season and nine days in Ponds E and Delta during the 1961 breeding season. Since male green sunfish commenced spawning during the first or second day of occupancy, the periods of nest establishment coincided with periods of intense spawning.

In 1961, sunfish in Pond Delta (Text-fig. 4) commenced constructing nests three days later than the fish in Pond E (Text-fig. 3) and as a result the periods of nest construction of the two populations were out of phase. However, the nesting periods in the two ponds gradually came into phase and, by the seventh period, the day of maximum nest construction occurred on the same day.

The daily mean water temperature for Pond E and the percentage of possible sunshine are shown in Text-figs. 2 and 3. The latter data were obtained from the U.S. Department of Commerce Weather Bureau at Truax Field, Madison. There appears to be no relationship between the daily amount of sunshine and the occurrence of nesting periods. Field observations support this view; large numbers of green sunfish were observed constructing their nests and spawning on overcast as well as on sunny days. There does, however, appear to be a correspondence between water temperature and nesting periods. The peak of each period of nest establishment nearly always coincided with a rise in the mean water temperature. In Pond



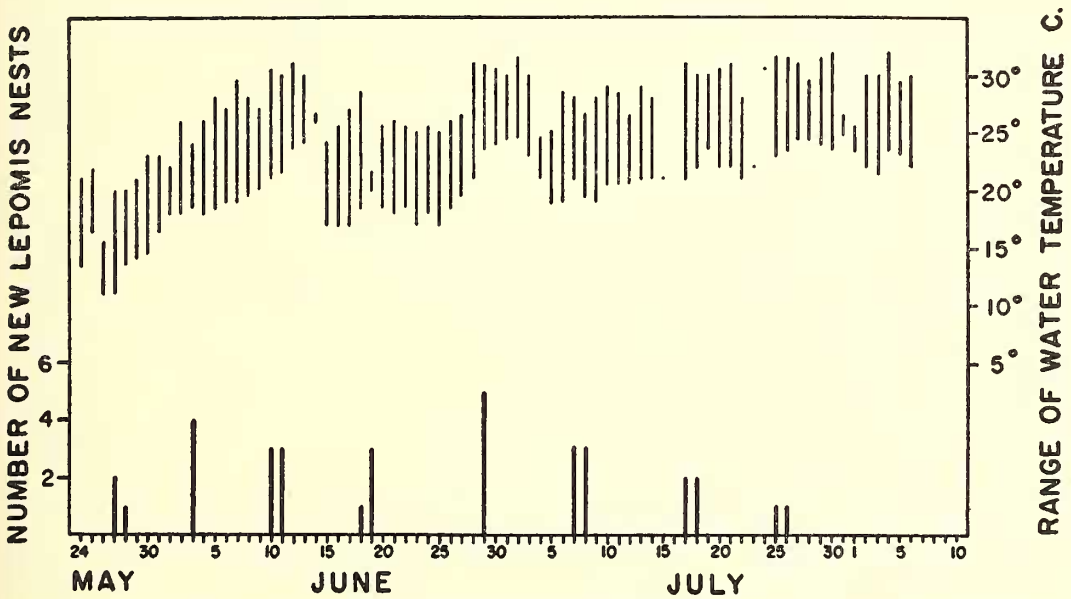
TEXT-FIG. 2. The number of nests constructed each day by *Lepomis cyanellus* in Pond E during the 1960 breeding season. Bars represent the number of nests constructed by *Lepomis;* upper line the percent. of possible sunshine; and lower line the mean water temperature.



TEXT-FIG. 3. The number of nests constructed each day by *Lepomis cyanellus* in Pond E during the 1961 breeding season. Bars represent the number of nests constructed by *Lepomis;* upper line the percent. of possible sunshine; and lower line the mean water temperature.

Delta, a similar correspondence may be seen (Text-fig. 4). In addition, the longest intervals between nesting periods occurred during periods of generally decreasing water temperature. For example, the longest interval recorded between two nesting periods occurred in Pond E in 1961 between July 8 and July 17, a time characterized by generally declining water temperature.

A change in water temperature has been considered to be an important factor controlling the



TEXT-FIG. 4. The number of nests constructed each day by *Lepomis cyanellus* in Pond Delta during the 1961 breeding season. Lower bars represent the number of nests constructed by *Lepomis;* upper bars the range of water temperature.

initiation of spawning in many species of fish (Aronson, 1957). In the current study, however, steep rises in water temperature were recorded in both ponds during times when no or few nests were constructed; hence, it appears that factors other than temperature also were involved.

To examine the problem more thoroughly, the nesting habits of individually tagged male green sunfish were studied. On the first and second of June, 1961, 25 male green sunfish were removed from their nests on the spawning grounds of Pond E by hook and line, tagged and returned to the pond. Each of the 25 males could be identified from the shore by the color, shape, and size of a plastic tag attached to its back by means of a stainless steel wire inserted just anterior to the first dorsal ray.

Many of the tagged male green sunfish were caught from Pond E by poachers. Records are complete up to July 10 as no fishing occurred until this time; between July 10 and 29 poaching was detected on five occasions.

Nineteen of the 25 male green sunfish constructed nests during each of the first five nesting periods and the majority of the fish that had not been caught constructed nests during the following two nesting periods; two males constructed nests during all eight periods of nest establishment (Table I). Thus, the tagged male sunfish tended to construct nests during each of the nesting periods.

The male sunfish tagged in Pond E were all relatively large fish, their sizes ranging from 118 mm. to 181 mm. Although the basic breeding element of the population in Pond E consisted of fish in this size range, late in the season smaller males entered the breeding population in large numbers. These males constructed nests in phase with the larger fish. In a pond, not previously mentioned (Pond B), I observed, in 1960, one-year-old fish spawning. The spawning period for these small males was late July or early August, whereas in that same year, the large male sunfish in Pond E commenced spawning in late May.

The nesting habits of four males which had been fin-clipped and stocked in Pond Theta in April, 1961, were also recorded. Only the largest of these bred throughout the season (Table I). Each of the large males (about 150 mm. T.L.) occupied one of the two gravel-filled spawning boxes which had been placed at opposite ends of the pond at the beginning of the season. These two large fish vigorously defended the entire spawning box, hence the two small males constructed their nests in the muck. The breeding periods of these sunfish were not synchronized as were those of the fish in Ponds E and Delta. However, the two large males tended to construct nests at somewhat regular intervals. In both cases the average frequency of nest establishment was nine days, which is the same frequency as that determined for the populations in Ponds E and Delta.

The lack of synchronization in the breeding behavior of the sunfish in Pond Theta may have resulted from the failure of these fish to breed in colonies. The nests in Theta were widely spaced, those of the two large males being at opposite ends of the pond, whereas the nests in Ponds Delta and E were nearly all arranged in colonies. In Delta the males were smaller (about 110 mm. T.L.) than those in Theta and as many as four males maintained nests in one spawning box simultaneously.

That synchronization in the breeding periods of green sunfish is correlated with colony formation is also indicated by data collected from Pond D in 1960. Nests were initially constructed on May 23 but, unfortunately, daily tabulations of new nests were not kept until June 18. During this time, however, I noted that nests were arranged in a compact colony, constructed at intervals and located in one segment of the spawning grounds. The colonies continued to form in the same region of the pond until July 18; thereafter the site was no longer used (Text-fig. 5). Because of a drop in water level, this area may have become too shallow for nest construction. After July 18 the nests were no longer located in a single large colony but were arranged in various regions of both cinder dams, alone, in pairs or in groups of three. When the nests were no longer arranged in a single compact colony, the synchronization of the breeding periods ceased.

Two females from Pond E were tagged on June 1, 1961, and were observed mating during several spawning periods. One was observed on the spawning grounds during three of the periods of spawning, the other during six periods. Thus it appears that female green sunfish mate during more than one spawning period.

Homing and Nest Recognition.—The location of the nests constructed by each of the 25 tagged male green sunfish in Pond E was marked on a map. The distance between nests was measured in the order of their occurrence during the season, that is, the distance between the first and second nests constructed by a given fish, its second and third, etc. Only the component of the distance between nests which was parallel to the shore line was tabulated, since the dis-

TABLE I. NESTING RECORDS OF 25 MALE LEPOMIS CYANELLUS FROM PONDS E AND THETA

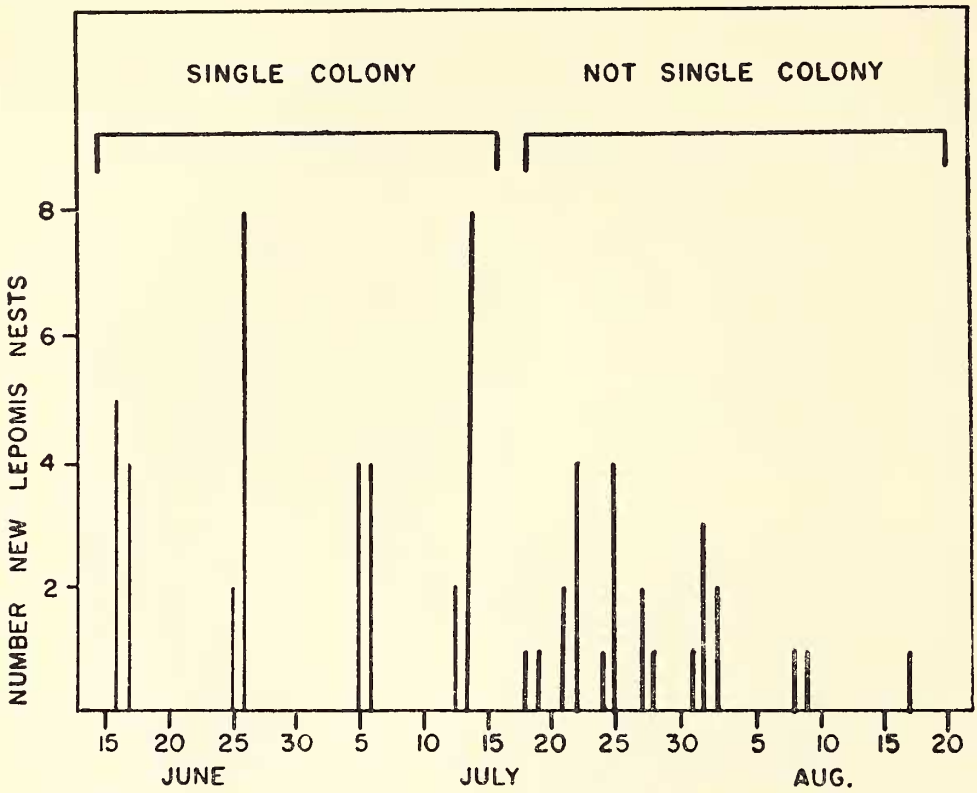
	May			June			July			August
	10	20	30	10	20	30	10	20	30	10
POND E				Nooooooo..Nooooooo.Nooo.....Nooooo...Noo*						
				Nooooooo..Nooooo..Nooooo.....Nooooo...Noooooo...*						
				Nooooooo.Nooooooo..Nooooooooo.Nooooo...Nooooo*						
				Nooooooooo.Nooooo...No.....NooooooN..Nooooo*						
				Nooo.....Nooooooo.Nooooooooo.NNo.....Nooooo*						
				Noo.....No.....NooooooooNooooo...Nooooo*						
				NooooooooNNooooo...Nooooo....Nooooo....Nooooo*						
				Nooo.....Nooooo.Nooooo....No.NNooooo.Nooo.*						
				N.....Nooooooo.NooooooooooNooooo...NNooooo*						
				N.....Nooooo...NoooooooooooNo.....Nooo.*						
				Nooooooo.....Nooooo*						
				Nooo.....N.....Nooooooo.Nooooo...Nooooo*						
N=New nest				Noo...NN....Noo.Nooooo.....Nooooo...Noooooo...Nooooo..Nooooo.						
				NooooooNNooooooooNooooo.....Nooooooo..Nooooo.....						
o=Nest occupied				N.....No.....N.....Noo.....						
				Nooooooo.Nooooooo..Nooooooooo..Noo.....Nooooooo.....N.....						
.=Nest not occupied				Nooooooo.Nooooooo..Nooo....N.Nooooooo...Nooooooo...Noo.....Nooo.....N.....						
				Nooooooo...Nooooo...Nooooooooo.....Nooo.....Nooo.....						
				N.....Nooo.....No.....						
*=Fish caught				Noo..Nooooooo.Nooooooo.....						
				Nooooooo..Nooooo...NooooooooNooo.....Noo.....						
				Noo.....Nooooooo..Nooooooo.Nooooo...Nooooooo.....N.....N.....						
				NooooooooNooooooooNooooooooooNoo...Nooooooooooo...Noooooo..No.						
				Nooooooo....Nooooo.Nooooo.....Nooooo..Nooooooo.....Noo...*						
				Nooooooo.Nooooooo....No.....NNooooo...Nooooooo.N..Noo....Nooooo.....N.....						
POND THETA										
Nooo....Nooooo.....Nooooooo.NooooN.NNooooooooo.....NooooNoooNooooooN....Nooooo.....Nooooooo.										
		Nooo...NooooooN.NooooN.Noo...N...Nooooo.No.Nooooooo.Nooooooo..N.....								
		Noo.....N....								
		Nooo.Noo..								

N=New nest

o=Nest occupied

.=Nest not occupied

*=Fish caught



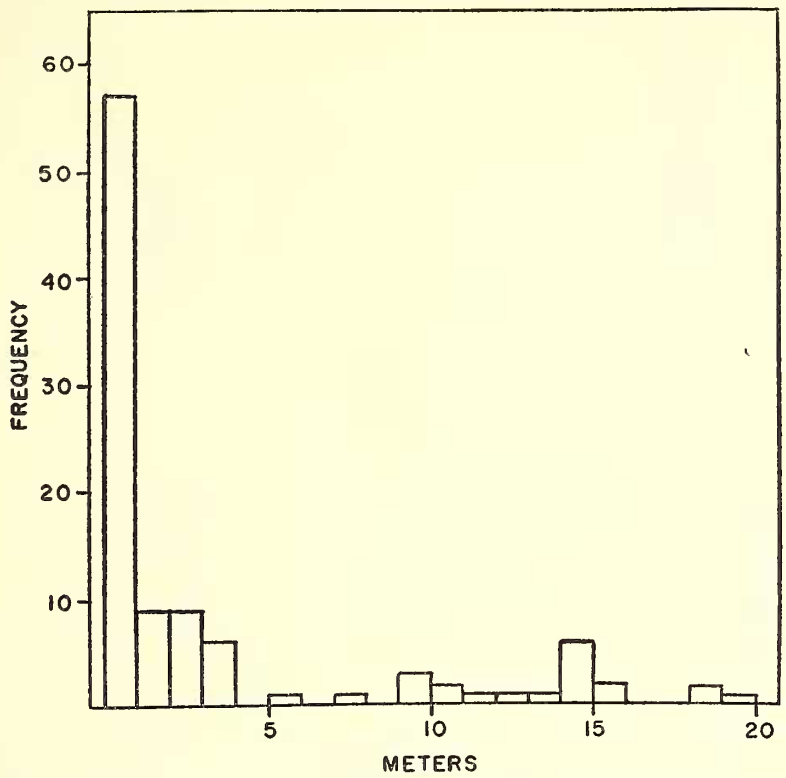
TEXT-FIG. 5. The number of nests constructed each day by *Lepomis cyanellus* in Pond D during the 1960 breeding season. *Lepomis* commenced constructing nests on May 23 but records were not kept until June 16. Bars represent the number of nests constructed; first bracket encloses period that nests were constructed in a single colony; and second bracket encloses period that nests were arranged alone, in pairs, or in groups of three.

tance at which a nest was located from the shore was strongly influenced by variations in the slope of the dam and by fluctuations in the water level of the pond. More than half of the nests were located within 1 meter from the previous nest (Text-fig. 6). Only a few instances of a male sunfish using exactly the same nest site were noted; usually a new nest was located near but not in exactly the same location as the old one. Some of the tagged males constructed nests in sunfish colonies, some outside. Nests were constructed along the entire length of the dam, hence the proclivity of a male sunfish to nest in a particular region was not the result of a lack of suitable substrate. It appears that male sunfish, while occupying a nest, learned to recognize regions of the spawning grounds and this familiarity with a small area influenced the location of subsequent nests.

The environmental references used by male green sunfish to identify regions in the spawning grounds have not been investigated. However, Schwassmann (1958)[3] performed a few experiments on the factors involved in the recognition of nest site by male green sunfish. Gravel covered pans, placed by Schwassmann on the spawning grounds, were used by male green sunfish as a spawning site. He found that if the pans were rotated 180° a male did not occupy his old nest, even when it contained eggs or fry, but occupied a new area on the pan which was located in the same position as the old nest. If, however, the position of small stones and sticks located around the pan was changed, the fish remained in the general vicinity of the pan but appeared to be disorientated. As long as these small landmarks were intact the fish showed little hesitation in occupying the new site, and in one case a male sunfish spawned on the day following the rotation of the pan.

Using the same method as Schwassmann, the

[3]Schwassmann, H. O. Unpublished field notes (Arboretum, Gardner Ponds). Hydrobiology Laboratory, University of Wisconsin.



TEXT-FIG. 6. Frequency distribution of the summation of the distance between each nest constructed by each of 25 tagged male *Lepomis cyanellus* in Pond E during the 1961 breeding season.

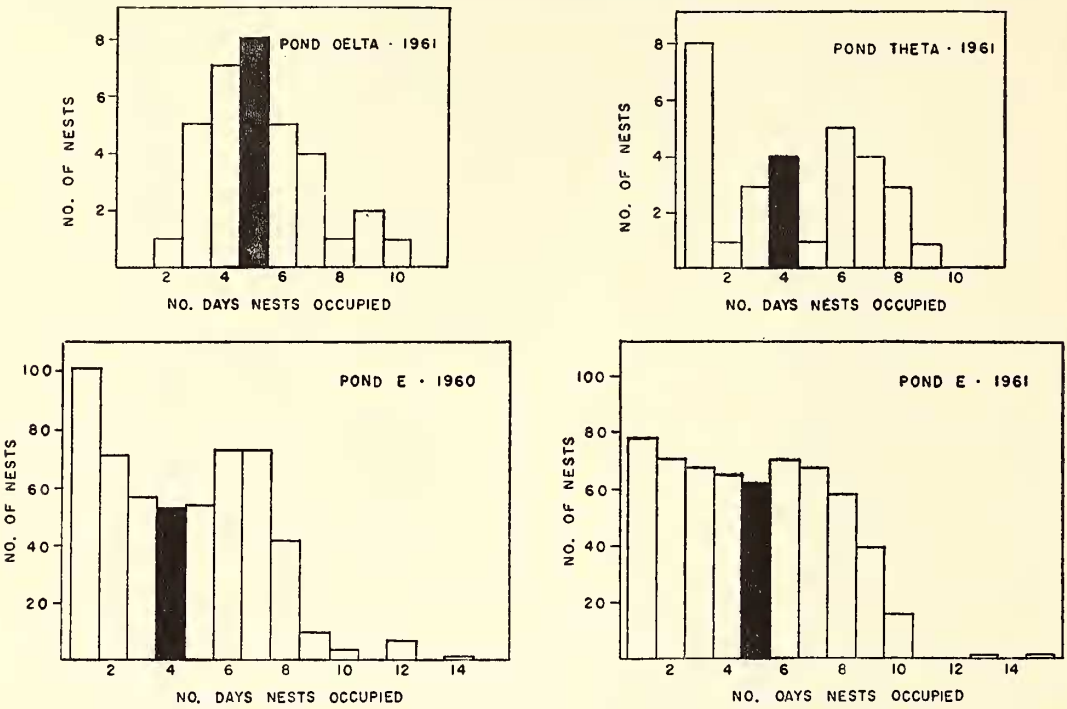
author found that if a nest and its associated landmarks were transferred 1 to 2 meters across a sunfish colony, the male sunfish would continue to occupy the nest. However, after the nest was displaced the male first returned to its former position in the colony, then swam to the new nest site and for a time oscillated between the two sites. Schwassmann, and later myself, covered sunfish nests with gravel-covered pans. The male was able to locate the occluded nest and maintained a position either alongside or over the pan.

It appears from these observations that neither the nest nor the young located in it are necessary for nest recognition. Small landmarks in the vicinity appear to play a major role in nest recognition and perhaps landmarks of this type are used by males to locate small areas on the spawning grounds. There is a clear indication, both from nesting records and from the observations cited above, however, that they are able to identify larger areas without the use of these small landmarks. The identity of these stimuli remains unknown.

Duration of Nest Occupancy.—The length of time green sunfish remained on their nests was tabulated for Pond E during the 1960 season and for Ponds E, Theta and Delta during the 1961 season. During the latter season all of the nests constructed in three of the eight periods of nest establishment in Pond E were omitted from the tabulation, because a large number of nesting males were caught by poachers during these periods.

The majority of the nests were occupied for four or more days. Very few males remained on their nests longer than nine days (Text-fig. 7). Occasionally males continued to occupy the same nest site for quite long periods of time. They periodically cleaned and reshaped their nests, however, and such reconstructed nests were tabulated as new nests.

The period that males remained on their nests did not necessarily correspond to the length of time required for the young to become free swimming. Larvae reared from eggs in the laboratory at 27 to 28° C. never became free swimming earlier than seven days after oviposition, while the median period of occupancy for the males was either four or five days (Text-fig. 7). A possible interpretation of these findings is that the age distributions of nests are com-



TEXT-FIG. 7. Frequency distribution of the length of time each nest was occupied by *Lepomis cyanellus* in Pond E in 1960 and 1961, and Ponds Delta and Epsilon in 1961. Dark bar indicates the median class.

posed of two classes: nests which tend to be occupied for a time sufficient for the young to be free swimming, and nests which tend to be abandoned soon after their construction. The bimodal age distribution of the nests constructed in Ponds E and Theta supports this interpretation; modes are present on the first and on the sixth or seventh day of occupancy.

Premature desertion of nests by male centrarchids has often been attributed to a rapid decline in water temperature (Latta, 1957). The first eight nests constructed in Pond E in May of 1961 were all deserted on the day following their construction and this coincided with a very steep drop in water temperature (Text-fig. 3). However, only on this occasion did it seem likely that a drop in water temperature was responsible for abandonment.

In some cases, the aggressive behavior of large male sunfish may be responsible for the short term occupancy of nests by small males. For example, a very small male (less than 5 cm. T.L.) was observed spawning on the ridge between the nests of two larger males. The absence of the small fish on the following day probably was the result of the attacks of the two larger males. Sometimes a large male drove a smaller male from its nest and occupied both its own and the appropriated nest at intervals for a day. In these cases it seems likely that the subsequent nest abandonment by the small male resulted from the actions of the larger male.

Large males occasionally dug several nests prior to spawning (Table I). These "trial" nests contributed to the number of nests deserted after one day's occupancy.

Discussion

The reproductive behavior of the green sunfish appears to be typical of the Family Centrarchidae. The findings in the pertinent literature for *Lepomis* summarized by Breder (1936) are generally in accord with the observations recorded in this report.

Entirely new was the discovery that there was a cyclical component in the breeding periods of populations of green sunfish. The nesting and spawning periods occurred at an average frequency of eight or nine days during the breeding season and never varied more than two days from the average frequency.

The frequency of nesting periods of the green sunfish population seemed to be controlled primarily by water temperature and changes in the reproductive state of the male sunfish. Nesting periods were nearly always initiated during

a time of rising water temperature, and the interval between two periods of nest construction tended to be longer during a period of decreasing water temperature. However, a rise in water temperature did not coincide with the initiation of a nesting period unless the temperature rose at least six days, or more frequently eight or nine days, after the start of the previous period. Because about half of the males deserted their nests by the fifth day of occupancy, the delay in the onset of a nesting period probably was not the result of a lack of male sunfish nor a deficiency in substrate. It appears, therefore, that this delay was a function of the time required for a male to proliferate a new supply of milt and for the appearance of concomitant changes in sexual motivation. Several field observations support this view: (1) during the interval between periods of nest establishment I attempted to obtain milt from nesting males and had no success and (2) males which occupied a nest continuously through several breeding periods would, prior to each spawning period, dig in and clean their nests.

An eight- or nine-day cycle of sexual development in male sunfish would adequately explain the frequency of the breeding cycles of the sunfish observed in this study. However, this hypothesis alone is not a sufficient explanation for the synchronization of the breeding periods of a population unless all males commenced breeding at the same time at the beginning of the season. Since this was not the case, it is necessary to hypothesize an additional mechanism for the synchronization of the breeding periods of male sunfish.

The synchronization may in part result from a stimulatory effect of spawning males. Females and non-nesting males were attracted to and aggregated around the nests of spawning males. I suspect that the spawning male stimulated the non-nesting males in the aggregation to construct nests and subsequently to spawn. In all the ponds fish assembled near the nests of spawning males, but only when nests were arranged in colonies did the breeding behavior become synchronized.

It is possible that the first male sunfish to commence digging nests stimulates other males to begin nest construction. Aronson (1945, 1951) has shown that the mere presence of a *Tilapia* in an adjacent aquarium markedly increased the number of times a female *Tilapia* spawned. In the current study, however, aggregations of males were observed only around the nests of males that were spawning rather than around the fish that had just begun to construct their nests.

In summary, my hypothesis is: individual male green sunfish have a somewhat regular cycle of gonad development and reproductive behavior during the breeding season; water temperature may have a stimulatory or inhibitory effect on the initiation of these breeding periods; social facilitation in nesting sunfish produces a synchronization of breeding periods.

It seems unlikely that all centrarchids show breeding cycles of the kind observed in this study; the largemouth bass, for example, sometimes has only one breeding period each year (James, 1946; Kramer & Smith, 1962). On the other hand, those species with a prolonged breeding season that construct nests in colonies may show a cyclic breeding pattern as does the green sunfish.

Summary

1. The reproductive behavior of the green sunfish, *Lepomis cyanellus,* is described with particular emphasis on the frequency of nest construction.

2. Males aggregated near the nests of the first males to construct nests and spawn. Some of these males later constructed nests near the original nest, thus forming colonies.

3. The nesting periods of sunfish breeding in colonies were synchronized and occurred at an interval of approximately eight to nine days. If males failed to nest in colonies, no synchronization of nesting periods was evident.

4. A male sunfish tended to construct a series of nests in the same region; more than half of the nests constructed by 25 males were located within a meter of their previous nest.

5. Nest recognition by males appeared to be partially dependent upon the presence of small landmarks near the nest site.

6. The length of time that nests were occupied by male green sunfish varied from 1 to 15 days. Histograms plotted from these data did not form a normal distribution but tended to be bimodal. The possible significance of these data is discussed in the text.

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